TRANSFER OF CHAETOPAPPA ELEGANS TO IONACTIS (ASTERACEAE: ASTEREAE)

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ABSTRACT

Chaetopappa elegans, narrowly endemic to the White Mountains of southcentral New Mexico, is better accommodated in morphology and chromosome number within the genus Ionactis. The transfer is made with the nomenclatural combination Ionactis elegans comb. nov. In a review of chromosome numbers in Chaetopappa and Ionactis, it is concluded that the base numbers of the two genera are x=8 and x=9, respectively. The closest relative of Chaetopappa is the ditypic genus Monoptilon (x=8), while Ionactis is hypothesized to be a basal member of the Heterotheca group (x=9).

KEY WORDS: Ionactis, Chaetopappa, chromosome numbers, Astereae, Asteraceae, New Mexico

In their investigation of possibilities for the generic placement of a distinctive and previously undescribed species of the White Mountains in southcentral New Mexico, Soreng & Spellenberg (1984) reasonably narrowed to the three most likely candidates: Chaetopappa DC., Ionactis E. Greene, and Erigeron L. (see Nesom 1988, 1989, and Nesom & Leary 1992 for taxonomic summaries of these genera). Their choice was Chaetopappa (C. elegans Soreng & Spellenberg), initially on the basis of its strongly graduated involucres, keeled phyllaries with hyaline margins, and prominently double pappus, but also in large part apparently because they felt the species could justifiably be absorbed into a seemingly more heterogeneous Chaetopappa after being rejected from both Erigeron and Ionactis.

Chaetopappa elegans is unequivocally excluded from Erigeron by its combination of strongly carinate phyllaries, low number of disc flowers per head, disc style branches with linear-lanceolate collecting appendages and long, flexuous collecting hairs, and by its glandular achenes. Soreng & Spellenberg

(1984, p. 4) eliminated their new species from *Ionactis* on the basis of its "habit, absence of rhizomes, reduced inflorescence, nature of the chlorophyllous zone of the phyllaries, and the absence of fine scabrous pubescence." In contrast, however, C. elegans produces a set of characteristics that are anomalous within Chaetopappa: loose, crinkly stem hairs; alveolate receptacles; ray flowers with relatively long, blue (fresh), showy ligules; narrowly lanceolate style appendages of the disc flowers; strongly oblique carpopodia; a relatively large number of pappus bristles (not 5 or based on a multiple of five); and a chromosome number based on x=9. Except for the carpopodial morphology and chromosome number, these were noted by Soreng & Spellenberg either as anomalous within Chaetopappa or as characteristic of Ionactis. Further, as noted by Soreng & Spellenberg (p. 1), C. elegans occurs to the north of other Chaetopappa and in a different habitat. In all of these features, the species is accommodated within Ionactis (Nesom & Leary 1992).

With respect to the habit of Chaetopappa elegans, Soreng & Spellenberg (1984, p. 3) provided this description: "Densely cespitose perennial, probably from a taproot, the perennating stems from the crown slightly woody, vertically or obliquely much-forked, often subrhizomatous." Ionactis alpina (Nutt.) E. Greene usually is distinctly rhizomatous but sometimes may appear taprooted, and it is otherwise very similar in habit as well as inflorescence (monocephalous stems) with C. elegans. Close matches of phyllary morphology also are found between C. elegans and species of Ionactis. The leaf surfaces of I. linariifolia (L.) E. Greene sometimes are minutely, barely hispidulous and approach the other three species in this respect, although commonly the leaves are nearly as smooth as in C. elegans. The stem hairs of C. elegans are somewhat larger than in species of Ionactis, but they are homologous (all apparently are Type B trichomes [Nesom 1976], vs. Type A in other Chaetopappa).

Chaetopappa hersheyi S.F. Blake is distinctive within Chaetopappa (as observed by Shinners 1946, Van Horn 1973, and Soreng & Spellenberg 1984) in its compact, caespitose habit, cauline leaves densely arranged and grading into the involucral bracts, and its solitary heads. Its resemblance to C. elegans in these features suggests that a phylogenetic connection might be found between the two, but in diagnostic characters, especially of style appendages, pappus, and chromosome number, C. hersheyi is similar to other typical Chaetopappa and different from C. elegans. Chaetopappa hersheyi is particularly similar to C. (Leucelene) ericoides (Torrey) Nesom in its densely arranged, coriaceous, apically spinulose leaves with a thick, raised midvein on the lower surface, the basal leaves often persistent, and its solitary heads. The habit of the former could have been derived from the latter by a shortening of the stems with condensation of the internodes.

Ionactis is hypothesized to be a basal member of the goldenaster lineage, Heterotheca Cass. and its relatives (Nesom & Leary 1992). The closest relative of Chaetopappa appears to be the ditypic genus Monoptilon Torrey & Gray,

of southern California and adjacent areas, on the basis of their common production of broad, scarious margined phyllaries, white rays, short style (disc) appendages, double pappus with a very strongly differentiated inner and outer series, and base chromosome number of x=8. Chaetopappa was merged with Pentachaeta Nutt. by Keck (1958), but in a detailed study, Van Horn (1973) regarded them as generically distinct. Instead, Pentachaeta and Tracyina S.F. Blake are almost certainly closely related (Blake 1937; Van Horn 1973), and these two may share close ancestry with the genus Rigiopappus A. Gray, although the latter is somewhat anomalous in the group. Plants of all three genera are primarily Californian annuals with long style (disc) appendages, monomorphic pappus, and base chromosome numbers of x=9.

While Ionactis and Chaetopappa apparently are not closely related to each other within the Astereae, it is of interest to note that both have a tendency to produce sterile disc ovaries and glandular achenes, both uncommon features among other North American Astereae. In Ionactis, sterile disc ovaries occur only in I. caelestis Leary & Nesom; in Chaetopappa, however, a strong tendency for this occurs at least in C. asteroides, C. effusa, and C. hersheyi. The peculiar morphology of the disc style branches (lack of stigmatic papillae) noted in C. effusa by Van Horn (1973) is a concomitant of such sterility. The most significant and consistent morphological differences that distinguish Chaetopappa and Ionactis are summarized in the following couplet.

Chromosome numbers in Ionactis and Chaetopappa

Chromosome counts based on x=9 have been made for three species of lonactis: I. caelestis (Nesom & Leary 1992, n=9); I. alpina (Solbrig et al. 1969, n=9 and n=18; Semple 1985, n=9); and I. linariifolia (Mehra et al. 1965; Mehra & Remanandan 1974; Hill 1978; Jones 1980; Semple & Brouillet 1980; Semple et al. 1983; Semple 1985; Semple et al. 1992; all n=9). The chromosome number of I. stenomeres (A. Gray) E. Greene apparently has not been reported.

Nine species of Chaetopappa, representative of nearly the complete range of morphological variation within the genus, are known to have a chromosome number based on x=8. Both diploids and tetraploids are known within two species. Only C. plomoensis B. Turner (closely similar to C. parryi) and C. keerlioides Shinners (intermediate in some respects between C. parryi and C. effusa) remain uncounted. A complete accounting of published chromosome numbers in Chaetopappa is presented here.

- Chaetopappa asteroides (Nutt.) DC. (Smith 1964, Van Horn 1973, Zhao & Turner in prep.; n=8)
- Chaetopappa bellidifolia (Gray & Engelm.) Shinners (Zhao & Turner in prep.; n=8)
- Chaetopappa bellioides (A. Gray) Shinners (Turner et al. 1961, Turner & Flyr 1966, Powell & Sikes 1970, Van Horn 1973, Keil & Pinkava 1976, Strother 1976, Turner 1978; n=8, n=16, n=9(?) see comments below)
- Chaetopappa effusa (A. Gray) Shinners (Zhao & Turner in prep.; n=8, see below)
- Chaetopappa ericoides (Torrey) Nesom (De Jong & Longpre 1963, Solbrig et al. 1969, Strother 1972, Keil & Pinkava 1976, Powell & Powell 1977, Semple 1980, Strother 1983, Sundberg 1983, Ward 1983, Semple 1985, Ward & Spellenberg 1986 (34 counts), Ward & Spellenberg 1988; n=8, n=16)
- Chaetopappa hersheyi S.F. Blake (Ward & Spellenberg 1986; n=8)
- Chaetopappa imberbis (A. Gray) Nesom (reported here; n=8: population voucher is Nesom 6224 [TEX] from Guadalupe County, Texas)
- Chaetopappa parry: A. Gray (Zhao & Turner in prep.; n=8)
- Chaetopappa pulchella Shinners (Turner et al. 1973; n=8) see comments below)

The previous report of n=9 for Chaetopappa bellidifolia (Solbrig et al. 1964) clearly was intended to refer to C. bellidiflora (E. Greene) Keck (= Pentachaeta bellidiflora E. Greene), which is endemic to a few Pacific coastal counties of California, including the locality of the voucher for the chromosome report. All taxa of Pentachaeta have a chromosome number of n=9 (Van Horn 1973); there is no aneuploid variation within the genus.

Two counts of n=9 have been reported for C. bellioides (Turner et al. 1961, Turner et al. 1973) among eight other published counts for the species of n=8 or n=16. The voucher for the 1961 count is clearly C. bellioides (TEX); the

voucher for the 1973 count, however, is a specimen of C. pulchella (TEX), and the chromosome number evidently was erroneously transcribed for publication, since the count was marked in Turner's notebook as well as on the specimen as "n=8 II." Two other counts of n=9 specifically recorded for C. pulchella (Turner et al. 1973) were in actuality counts for Erigeron pinkavii B. Turner (Powell & Turner 2299 and Turner 6010, vouchers for both in TEX), misidentified as C. pulchella.

A chromosome number of n=9 was noted for Chaetopappa effusa by Soreng & Spellenberg (1983), and this was repeated without documentation by Nesom (1988). I have not been able to locate the original source of this report and consider the report of n=9 in error, since recent counts by Zhao & Turner (in prep.) clearly show n=8 for C. effusa.

In summary, the base chromosome number of *Ionactis* is x=9. More than sixty-five published chromosome counts for *Chaetopappa* have been based on x=8; only a single count remains as a bonafide report of n=9 in *Chaetopappa*, and it is in *C. bellioides*, where published counts of n=8 also exist. The most widespread and variable species in the genus (*C. ericoides*) has the greatest number of counts, and all are based on x=8. The single report of n=9 for the genus may be explained as an error in counting, the occurrence of B-chromosomes, or as a true aneuploid variant. In the last case, however, there are numerous instances of aneuploid decrease in chromosome number in the Astereae and other tribes of Asteraceae, but in the Astereae I know of no example of aneuploid increase, and such a possibility seems unlikely within *Chaetopappa*. In any case, it seems clear that the immediate ancestor of *Chaetopappa* had eight pairs of chromosomes. The chromosome number of *C. elegans* (n=9, Soreng & Spellenberg 1984) is disparate in *Chaetopappa* but not in *Ionactis*.

Transfer of Chaetopappa elegans to Ionactis

The placement of Chaetopappa elegans within Ionactis, rather than Chaetopappa, provides a more refined hypothesis of the evolutionary relationships of this distinctive species. The significant degree of heterogeneity added to Chaetopappa by its inclusion was correctly surmised by Soreng & Spellenberg, while it is easily accommodated in Ionactis.

Ionactis elegans (Soreng & Spellenberg) Nesom, comb. nov. BASIONYM: Chaetopappa elegans Soreng & Spellenberg, Syst. Bot. 9:1. 1984. TYPE: UNITED STATES. New Mexico: Lincoln County, Eagle Creek Canyon, on the NE flank of Sierra Blanca, 105° 45′ W, 33° 25′ N, T10S, 11 Jul 1982, R. Soreng, R. Spellenberg, & D. Ward 2026 (HOLOTYPE: NY; Isotypes: K,NMC,TEX!).

With the addition of *Ionactis elegans*, the genus comprises five species (Nesom & Leary 1992). Within *Ionactis, I. elegans* is distinguished from the other taxa by a combination of characters: a relatively reduced, apparently tap rooted habit, persistent basal leaves, monocephalous stems, eglandular herbage, glabrous leaf surfaces, short disc corollas with glandular lobes, and glandular achenes. Of these features, compared to the other species, only the persistent nature of the basal leaves is unique to *I. elegans*.

Ionactis elegans is most similar to I. alpina and I. stenomeres in its monocephalous stems, cauline leaves well differentiated from the phyllaries, and phyllaries with hairy midregions. Both of the latter species are similar between themselves in long achenes (5-6 mm long, vs. 2-3 mm in the other species) and fibrous roots, and both are species primarily of the northwestern United States, separated by long distances from the geographic locality of I. elegans. The wide morphological divergence among all of the species of Ionactis, their distribution on both east and west sides of the continent, their otherwise widely disjunct distributions, and the extremely narrow (probably relictual) endemism of two of them, suggest that the active evolutionary period for the genus occurred in a relatively ancient period.

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